Photochemistry and Photobiology, 2005, 81: 1021–1025

Symposium-in-Print: Ultraviolet Radiation and Terrestrial Ecosystems Introduction

Ultraviolet Radiation and Terrestrial Ecosystems†

Donald T. Krizek*[1] and Linda Chalker-Scott[2]

[1]Sustainable Agricultural Systems Laboratory, Animal and Natural Resources Institute, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, MD
[2]Washington State University Puyallup Research and Extension Center, Puyallup, WA

Received 18 August 2005; accepted 18 August 2005; published online 23 August 2005 DOI: 10.1562/2005-08-18-RA-654

INTRODUCTION

We are pleased to bring this Symposium-in-Print on Effects of Ultraviolet Radiation on Terrestrial Ecosystems to the readers of Photochemistry and Photobiology. Six of the 10 articles contained in this Symposium-in-Print are based on invited presentations given at the symposium on ''Effects of Ultraviolet Radiation on Terrestrial Ecosystems,'' held during the American Society for Photobiology (ASP) Meeting in Seattle, WA on 10–14 July 2004. One of the articles is based on a presentation given at a symposium on ''Solar UV Radiation Effects on Plants: Interactions with Abiotic and Biotic Stress Factors'' held at the 13th International Photobiological Congress in San Francisco, CA on 16 July 2000 and two of the articles are based on presentations given at the ASP Symposium on ''Effects of Ultraviolet Radiation on Terrestrial Ecosystems'' in Baltimore, MD, MD on 5–9 July 2003. One of the invited papers was not presented at an ASP Symposium but was included because of its timeliness and relevance.

This Symposium-in-Print is the second in the series of papers published in this journal on Ultraviolet Radiation and Terrestrial Ecosystems during the past 2 years. The first Symposium-in-Print was published in the May 2004 issue of *Photochemistry and Photobiology* (1). The present ASP Symposium was held to provide a current perspective of research findings obtained since 2000. Partial funding for both the current and previous ASP Symposium was provided by the ASP and the Beltsville Area Director's Office, Beltsville Agricultural Research Center, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, MD. The articles presented in this Symposium-in-Print address both basic and applied aspects of UV research on terrestrial organisms and cover a range of topics that should be of broad interest to photobiologists, plant physiologists and other researchers.

The biological impact of stratospheric ozone depletion, brought about by inadvertent release of chlorofluorocarbons and other trace gases, and the attendant increase in biologically effective ultraviolet radiation on terrestrial and aquatic ecosystems has been of keen interest to researchers and policy makers since the late 1960s (2,3). Changes in stratospheric ozone levels and/or biologically effective ultraviolet radiation (UV_{BE}) have been recorded at a number of locations (4,5,6). Although the UV-B spectral band (280–315 nm) contributes less than 2% of the short-wave radiation received at the earth's surface, it is of critical importance to terrestrial species (7).

Two generalizations are beginning to emerge from field experiments conducted in natural and cultivated ecosystems. The first is that both ambient UV-B (7–10) and ambient UV-A (8,9,11) seem to have a measurable effect in reducing plant growth, especially in the case of herbaceous plants. The second is that changes in ambient UV-B levels may exert a large impact on interactions between plants and phytophagous insects (7,12–15).

Numerous studies have been published on the effects of ambient and enhanced UV-B radiation on terrestrial organisms (16–39). One of the major constraints to understanding the mechanisms that mediate the effects of ambient UV-B radiation is the fact that most studies conducted at the molecular level have been carried out in the laboratory using monochromatic UV-B sources (7) or under controlled environments in which the ratio of UV-B to photosynthetically active radiation (PAR) is unrealistically high (40).

It is often difficult to compare results because of technical difficulties in predicting, measuring and applying realistic UV-B levels; differences in irradiation protocols in field, greenhouse and growth chamber experiments; and failure to provide adequate levels of PAR and UV-A radiation (40).

In their invited review article, Furness and her coworkers (41) describe a number of experimental and analytical approaches that have been used to study the influence of enhanced solar UV-B radiation on plant competition. These include inverse yield-density models and allometric, neighborhood or size structure analyses that provide links between plant and ecosystem responses. They point out that these approaches differ in their abilities to extract information regarding competitive interactions and their morphological underpinnings. Relatively few studies have been carried out

* To whom correspondence should be addressed: Sustainable Agricultural Systems Laboratory, Animal and Natural Resources Institute (ANRI), Agricultural Research Service, U. S. Department of Agriculture, Building 001, Room 140, BARC-West, 10300 Baltimore Avenue, Beltsville, MD 20705-2350, USA. Fax: 301-504-8370; e-mail: krizekd@ba.ars.usda.gov

† Presented in part at the 32nd Annual Meeting of the American Society for Photobiology, 10–14 July 2004, Seattle, WA.

to investigate UV-B effects on plant competition, and most of these have used a replacement series approach.

Despite the paucity of studies, there is a general consensus that slight differences in UV-B–induced morphological responses of species grown within associations can alter canopy structure and thereby influence the interception of PAR and relative competitive ability. To make predictions and draw generalizations regarding the ecological influence of UV-B radiation on plant competition, Furness *et al.* (41) feel that long-term growth and regeneration studies are needed, using mixed-species associations. This is especially important in an agricultural system where elevated UV-B radiation levels can alter crop:weed competitive relationships, thereby impacting weed management strategies and crop productivity. In less intensely managed ecosystems, UV-B enhancement may alter community structure and/or species diversity.

Grant and Slusser (42) analyze the frequency of occurrence of high hourly UV-B exposures at northern midlatitudes during the 1997–2002 summer growing seasons (May through August) at five locations between 38° to 41° latitude in the U. S. Department of Agriculture UV-B Climate Network. Two different weighting functions are used to describe the amount of biologically effective UV-B radiation (UV-B_{BE}): one created by Caldwell in 1971 (16) designated UV-B_{BE} (1971); and an updated one created by Flint and Caldwell in 2003 (43,44) designated UV-B_{BE} (2003). The objective of the present study was to define characteristic high UV-B_{BE} exposures for plant effects researchers.

Grant and Slusser (42) point out that the long-term effects of brief events of high UV radiation on the growth and development of plants are relatively unknown. The use of UV-B exclusion studies in recent years has intensified the need to understand the frequency of occurrence of these short-term events because it is through these events that above average UV-B exposures occur. Evaluation of the typical intensity and duration of such exposures is critical to understand the biological effects of acute UV-B exposures. They found that days with high exposures of UV-B_{BE} (1971) and UV-B_{BE} (2003) were more common in the western United States than in the eastern United States. The frequency of occurrence of 2 or more days of high hourly UV-B_{BE} (1971) exposures increased from east to west, likely a result of both higher altitude and lower average cloud cover.

Krizek *et al.* (45) characterize the spectral properties of selected UV-blocking and UV-transmitting covering materials with a UV–VIS spectroradiometer or a UV–VIS spectrometer to provide workers and growers with guidelines for selecting suitable materials for use in studying the influence of ambient solar UV radiation on the production of tomatoes and other high-value crops in high tunnels. The study focuses on evaluating films that either block or transmit UV wavelengths below 380 nm to determine comparative growth, yield and market quality and to provide a tool for integrated pest management (IPM). Based on this survey, two contrasting covering materials of similar thickness and durability were selected and used to cover two high tunnels at Beltsville, MD, one a UV-blocking film and the other a UV-transmitting film. Comparative measurements were also made of selected glass and plastic materials that have been used in UV exclusion studies to provide investigators with baseline information for selecting suitable filters in future studies. The use of UV-blocking films as an IPM strategy has attracted considerable interest as a nonchemical approach to reducing the prevalence of insects and plant diseases in greenhouses and high tunnels (46,47) by interfering with the ultraviolet vision of insects (48).

Paul and his coworkers (49) studied plant response to plastic covering materials that had one of the following effects: (a) increased transmission of UV radiation compared with standard horticultural greenhouse covering materials; (b) decreased transmission of UV radiation; or (c) an increased ratio of red to far-red (R:FR) radiation, using lettuce as a model plant. The UV-transparent films and the films with an increased R:FR ratio both reduced leaf area and biomass of lettuce plants, indicating they can be used as potential alternatives to chemical growth regulators. The UV-opaque film increased growth suggesting that it might be useful for some crops; however, there were trade-offs in terms of certain food quality issues such as pigmentation and taste.

Paul *et al.* (49) also investigated the use of UV-transmitting and UV-blocking covering materials to alter plant pathogenicity. They found that increasing UV transmission inhibited the pathogenic fungus *Botrytis cinerea* as well as the disease biocontrol agent *Trichoderma harzianum*. Unlike *B. cinerea*, however, *T. harzianum* was very sensitive to UV-A radiation.

UV-B radiation is known to induce a number of photomorphogenic responses. These include leaf asymmetry, leaf thickening and cotyledon curling. The nature of the UV-B photoreceptor remains to be elucidated (40). In their invited article, Gerhardt *et al.* (50) construct an action spectrum of cotyledon curling in light-grown *Brassica napus* to characterize the UV-B photoreceptor that initiates this response. They also characterized cotyledon curling in *Arabidopsis*. Peak efficiency for this response is between 285 nm and 290 nm. UV-B induced changes in epidermal cells from *A. thaliana* cotyledons were assessed because these cells were felt to be the likely site of UV-B photoreception that leads to curling. Investigation of cellular structure, chlorophyll *a* fluorescence and chlorophyll concentration indicated that cotyledon curling was not concomitant with gross cellular damage or inhibition of photosynthesis, which only occurred in response to wavelengths shorter than 280 nm.

Gerhardt *et al.* (50) suggest that many UV-B effects are caused indirectly and may depend on UV-B mediated increases in reactive oxygen species (ROS) that either act as a signal in the UV-B transduction pathway or cause oxidative damage. They point out that the cotyledon curling response is impeded by ascorbate and cystine and ROS scavengers and promoted by hydrogen peroxide (H_2O_2), a ROS. They propose that following absorption by a UV-B chromophore, ROS are generated via photosensitization ultimately leading to cotyledon curling.

Shinkle *et al.* (51) examine the influence of short-term exposures of different UV wavebands on elongation and phototropic curvature of hypocotyls of cucumber seedlings grown in white light (WL) and dim red light (DRL). They investigated whether different wavebands within the UV-B region elicit different responses and whether simultaneously exposing the seedlings to both blue-light–enriched white light (B/WL) and UV-B irradiation reversed the effect of UV exposure, in a manner indicative of photoreactivation. They also determined whether responses in WL-grown plants were similar to those grown in DRL and examined the hypocotyl elongation response elicited by UV-C radiation.

Seedlings given brief exposure to UV-B radiation for 1–100 min at three different wavebands all showed an inhibition in hypocotyl elongation after 24 h. These investigators indicate that there appears to be a response to short wavelength UV-B radiation that is mediated by DNA damage, but through some rapidly acting mechanism more specific than conventional toxicity of DNA lesions. The recent study by Giordano *et al.* (37) linking inhibitory growth effects with increased DNA damage in *Gunnera magellanica* under realistic field conditions would tend to support the notion that plants have a system for sensing DNA damage and initiating cellular signals that are amplified to lead to changes in growth. Shinkle *et al.* (51) propose that in some cases DNA may act as a photosensor for UV-B radiation and that the regulatory events initiated by DNA damage could be photomorphogenic in nature.

Middleton and her coworkers (52) conducted a growth chamber experiment to determine whether ethylenediurea (EDU), a chemical shown to be protective against ozone pollution, could ameliorate foliar damage induced by UV-B radiation exposure in 'Roanoke' soybean (*Glycine max* L.) , a UV-B–sensitive cultivar, and whether these effects could be discriminated using fluorescence (F) observations. There were four treatment groups: control; biologically effective UV-B (18 kJ m^2 d^{-1}); EDU (500 μmol mol^{-1}); and both UV-B and EDU (UV/EDU). Measurements were made of photosynthetic pigments, F image system (FIS) images of adaxial surfaces in four spectral regions (blue, green, red and far-red) and F emission spectra of the pigment extracts produced at two excitation wavelengths, 280 nm (280EX) and 380 nm (380EX). Several fluorescence ratios from 280EX, 380EX and the FIS images successfully separated the low UV *vs* the high EDU group responses based on means alone, with intermediate values for controls and the combined UV/EDU groups.

A UV-B/blue emission ratio (F315/F420 [280EX]) and a ratio of emissions at two UV-A wavelengths: F330/F385 (280EX), was correlated with chlorophyll content. These two 280EX ratios were also linearly correlated with emission ratios produced by 380EX, such as the far-red/green ratio, F730/F525 and clearly distinguished the UV-B and EDU groups separately and bracketed the intermediate responses of the UV/EDU and control groups. The FIS images also captured anatomical spatial patterns across the leaf surfaces. The emissions of EDU-treated leaves exhibited the greatest variation in spatial patterns with the veins having elevated blue F and the leaf edges having enhanced R and FR. Their findings support the hypothesis that EDU substantially ameliorates UV-B damage to foliage in soybean.

Ruhland *et al.* (53) determined the influence of solar UV-B radiation on the growth, biomass production and phenylpropanoid concentrations of Antarctic hair grass (*Deschampsia antarctica*) and Antarctic pearlwort (*Colobanthus quitensis*) during the springtime ozone depletion season on the Antarctic Peninsula at Palmer Station from 7 November 1998 to 8 January 1999. These are the only two vascular plant species native to Antarctica. In their experiments, they grew two sets of potted plants of *D. antarctica* under wooden frames that were covered with Aclar to provide near-ambient UV-B treatment or with polyester (Mylar) to exclude ambient UV-B (reduced UV-B). A third set was left unfiltered to provide ambient solar UV radiation.

Relative growth rates and net assimilation rates were 41% and 40% lower, respectively, under near-ambient UV-B (Aclar) than under reduced UV-B (Mylar). The former group of plants produced 50% less total biomass and 47% less aboveground biomass than did the latter group of plants. The Aclar-filtered plants subjected to near-ambient UV-B also had a 29% lower elongation rate and 59% less total leaf area than did Mylar-filtered plants grown under reduced UV-B radiation. The reduction in biomass and total leaf area appeared to be largely a reflection of the reduction in leaf elongation rather than a reduction in photosynthesis per unit leaf area. Concentrations of insoluble p-coumaric acid and caffeic acid-soluble ferulic acids were 38%, 48% and 60% higher, respectively, under near-ambient UV-B than under reduced UV-B. There were no effects of UV-B on the concentration of insoluble or soluble flavonoids (53).

Recent measurements indicate that the levels of biologically effective UV radiation in North America have increased as a consequence of stratospheric ozone depletion. Over southern Canada, the ozone layer decreased an average of 6% from the late 1970s to 1990s (5). Based on conservative estimates, this translates to approximately a 12%–16% increase in biologically effective UV radiation. To determine the possible impact of elevated UV-B on representative woody species in British Columbia, L'Hirondelle *et al.* (54) selected 10 conifer species from a wide range in geographic locations and exposed them to supplemental UV-B. Because of logistical and budget constraints, the studies were confined to short-term experiments conducted in the greenhouse. They subjected plant material of two ages (germinants during the first growing season and seedlings during the second season) to four levels of biologically effective UV-B radiation, ranging from zero to three times ambient level (12 kJ m^{-2} d^{-1}) for up to 4 months.

Because UV-B radiation has been shown to induce cross-protection against other environmental stresses (55,56), L'Hirondelle and her coworkers (54) estimated frost hardiness and heat tolerance of conifer shoots from changes in chlorophyll fluorescence after exposure to test temperatures. The results varied considerably, depending on both genetic and environmental factors. Four species (yellow-cedar, Engelmann spruce, lodgepole pine and western red cedar) showed an increase in frost hardiness and two (grand fir and interior spruce) showed a decrease. Four species (Engelmann spruce, Sitka spruce, western red cedar and western hemlock) showed an increase in heat tolerance under elevated UV-B radiation. The main differences in stress tolerance observed were between plants receiving 0 and 12 or 0 and 4 kJ m^{-2} d^{-1} (ambient) UV-B radiation; there was no difference between 4 and 8 kJ m^{-2} d^{-1} (2 × ambient) levels. Although elevated UV-B increased temperature stress tolerance in certain species, this appeared to be offset by a decrease in biomass.

Caasi-Lit (57) describes experiments which she conducted in Australia to determine the effects of crude and partially purified extracts from UV-B–irradiated rice (*Oryza sativa* L.) leaves on the growth and development of the corn earworm, *Helicoverpa armigera* (Hübner). This is a polyphagous insect pest of considerable economic importance throughout the world. Fifty microliter droplets of a liquid diet containing different concentrations of the crude and partially purified extracts were fed to *H. armigera* neonates to determine possible short-term toxicity effects. A choice test using a solid artificial diet was conducted to determine larval feeding preferences and antifeedant effects.

Results of these studies showed that crude and partially purified extracts of UV-B–irradiated rice leaves demonstrated antifeedant, growth-inhibitory and antibiotic properties against this insect. At high concentrations, the extracts initially stimulated larval feeding but subsequently there were negative effects on pupal and adult traits, thereby reducing the reproductive potential of the adults. The partially purified extracts appeared to have antifertility properties because adults laid fewer eggs and of those laid, viability was lower. These results suggest that the flavonoids and/or other phenolics in UV-B–irradiated leaves that were extracted from the UV-B–resistant rice cultivar 'M202' had an adverse effect on the growth, development and reproduction of *H. armigera* (57). The influence of solar UV-B radiation in altering leaf quality and leaf herbivory is a subject that is of considerable interest because of its potentially significant impact on both native and agricultural ecosystems. Subtle changes in flavonoids, hydroxycinnamic acids and other phenolic compounds induced by solar UV-B radiation have been shown to exert a dramatic influence on herbivory in both herbaceous and woody species (15,36,58). If significant advances are to be made in understanding the biological impact of ambient and enhanced solar UV radiation, it is clear that future UV-B assessments must be done at multiple trophic levels.

We hope that this symposium-in-print will provide readers with exciting examples of current research being conducted at the molecular, cellular, organism and ecosystem level to assess the influence of ambient and elevated UV radiation on terrestrial ecosystems and will provide a stimulus for further work in this important area of photobiology.

REFERENCES

1. Krizek, D. T. and W. Gao (2004) Introduction: Symposium-in-Print—ultraviolet radiation and terrestrial ecosystems. *Photochem. Photobiol.* **79**, 379–381.
2. Solomon, S. (1999) Stratospheric ozone depletion: a review of concepts and history. *Rev. Geophys.* **37**, 275–316.
3. Zepp, R. G., T. V. Callaghan and D. J. Erickson III (2003) Interactive effects of ozone depletion and climate change on biogeochemical cycles. *Photochem. Photobiol. Sci.* **2**, 51–61.
4. Casiccia, V. W., J. Kirchhoff and A. Torres (2000) Simultaneous measurements of ozone and ultraviolet radiation, spring 2000, Punta Arenas Chile. *Atmos. Environ.* **37**, 383–389.
5. Environment Canada (2000) Stratospheric ozone thickness an indicator of srtatospheric ozone depletion for southern B.C. What is happening? Canadian Meteorological Centre, http://www.ecoinfo.ec.gc.ca/env_ind/region/ozone/ozone_e.cfm, accessed August 31, 2005.
6. McKenzie, R. L., L. O. Björn, A. Bais and M. Ilyas (2003) Changes in biologically active ultraviolet radiation reaching the earth's surface. *Photochem. Photobiol. Sci.* **2**, 5–15.
7. Ballaré, C. L. (2003) Stress under the sun: spotlight on ultraviolet-B responses. Editorial. *Plant Physiol.* **132**, 1725–1727.
8. Krizek, D. T., R. M. Mirecki and S. J. Britz (1997) Inhibitory effects of ambient levels of solar UV-A and UV-B radiation on growth of cucumber. *Physiol. Plant.* **100**, 886–893.
9. Krizek, D. T., S. J. Britz, and R. M. Mirecki (1998) Inhibitory effects of ambient levels of solar UV-A and UV-B radiation on growth of cv. New Red Fire lettuce. *Physiol. Plant.* **103**, 1–7.
10. Robson, T. M., V. A. Pancotto, S. D. Flint, C. L. Ballaré, O. E. Sala, A. L. Scopel and M. M. Caldwell (2003) Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytol.* **160**, 379–389.
11. Phoenix, G. K., D. Gwynn-Jones, J. A. Lee and T. V. Callaghan (2002) Ecological importance of ambient solar ultraviolet radiation to a sub-arctic heath community. *Plant Ecol.* **165**, 263–273.
12. Ballaré, C. O., M. C. Rousseaux, P. S. Searles, J. G. Zaller, C. V. Giordano, T. M. Robson, M. M. Caldwell, O. E. Sala and A. L. Scopel (2001) Impacts of solar ultraviolet-B radiation on terrestrial ecosystems of Tierra del Fuego (southern Argentina). An overview of recent progress. *J. Photochem. Photobiol. B: Biol.* **61**, 67–77.
13. Izaguirre, M. M., A. S. Scopel, I. T. Baldwin and C. L. Ballaré (2003) Convergent responses to stress, solar ultraviolet-B radiation and *Manduca sexta* herbivory elicit overlapping transcriptional responses in field-grown plants of *Nicotiana longiflora*[1[w]]. *Plant Physiol.* **132**, 1755–1767.
14. Paul, N. D. and D. Gwynn-Jones (2003) Ecological roles of solar UV radiation: towards an integrated approach. *Trends Ecol. Evol.* **18**, 48–55.
15. Rousseaux, M. C., R. Julkunen-Titto, P. S. Searles, A. L. Scopel, P. J. Aphalo, and C. L. Ballaré (2004) Solar UV-B radiation affects leaf quality and leaf herbivory in the southern beech tree *Nothofagus antarctica*. *Oecologia* **138**, 506–512.
16. Caldwell, M. M. (1971) Solar ultraviolet radiation and the growth and development of higher plants. In *Photophysiology*, Vol. 6 (Edited by A. C. Giese), pp. 131–177. Academic Press, New York.
17. Greenberg, B. M., M. I. Wilson, X.-D. Huang, C. L. Duxbury, K. E. Gerhardt and R. W. Gensemer (1997) The effects of ultraviolet-B radiation on higher plants. In *Plants for Environmental Studies* (Edited by W. Wang, J. W. Gorsuch and J. S. Hughes), pp. 1–35. CRC Press Lewis Publishers, Boca Raton, FL.
18. Caldwell, M. M., P. S. Searles, S. D. Flint and P. W. Barnes (1999) Terrestrial ecosystem responses to solar UV-B radiation mediated by vegetation, microbes and abiotic photochemistry. In *Physiological Plant Ecology*, the 39th Symposium of the British Ecological Society, University of York, 7–9 September 1998 (Edited by M. C. Press, J. D. Scholes and M. G. Barker), pp. 241–262, Blackwell Science, Oxford, UK.
19. Mazza, C. A., H. E. Boccalandro, C. V. Giordano, D. Battista, A. L. Scopel and C. L. Ballaré (2000) Functional significance and induction by solar radiation of ultraviolet-absorbing sunscreens in field-grown soybean crops. *Plant Physiol.* **122**, 117–125.
20. Ruhland, C. T. and T. A. Day (2000) Effects of ultraviolet-B radiation on leaf elongation, production and phenylpropanoid concentration of *Deschampsia antarctica* and *Colobanthus quitensis* in Antarctica. *Physiol. Plant.* **109**, 244–251.
21. Day, T. A. (2001) Multiple trophic levels in UV-B assessments—completing the ecosystem. *New Phytol.* **152**, 183–186.
22. Day, T. A. (2001) Ultraviolet radiation and plant ecosystems. In *Ecosystems, Evolution and Ultraviolet Radiation* (Edited by C. S. Cockell and A. R. Blaustein), pp. 80–117. Springer-Verlag, New York, Berlin.
23. Day, T. A., C. T. Ruhland and F. S. Xiong (2001) Influence of solar ultraviolet-B radiation on Antarctic terrestrial plants: results from a four year field study. *J. Photochem. Photobiol. B: Biol.* **62**, 78–87.
24. Hoffman, R. W., B. D. Campbell, D. W. Fountain, B. R. Jordan, D. H. Greer, D. Y. Hunt and C. L. Hunt (2001) Multivariate analysis of intraspecific responses to UV-B radiation in white clover (*Trifolium repens* L.). *Plant Cell Environ.* **24**, 917–927.
25. Rousseaux, M. C., A. L. Scopel, P. S. Searles, M. C. Caldwell, O. E. Sala and C. L. Ballaré, (2001) Responses to solar ultraviolet-B radiation in a shrub-dominated natural ecosystem of Tierra del Fuego (southern Argentina). *Global Change Biol.* **7**, 467–478.
26. Rozema, J., R. Broekman, D. Lud, A. H. J. Huiskes, T. Moerdijk, N. de Bakker, B. Meijkamp and A. van Beem (2001) Consequences of depletion of stratospheric ozone for terrestrial Antarctic ecosystems: the response of *Deschampsia antarctica* to enhanced UV-B radiation in a controlled environment. *Plant Ecol.* **154**, 103–115.
27. Searles, P. S., S. D. Flint and M. M. Caldwell (2001) A meta analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* **127**, 1–10.
28. Björn, L. O. (2002) Effects of UV-B radiation on terrestrial ecosystems with special reference to the Arctic. In *UV Radiation and Arctic Ecosystems. Ecological Studies 153* (Edited by D. O. Hessen), pp. 93–121. Springer-Verlag, Berlin.
29. Day, T. A. and P. J. Neale (2002) Effects of UV-B radiation on terrestrial and aquatic primary producers. *Annu. Rev. Ecol. Syst.* **33**, 371–396.
30. Rozema, J., L. O. Björn, J. F. Bornman, A. Gaberščik, D.-P. Häder, T. Trŏst, M. Germ, M. Klisch, A. Gröniger, R. P. Sinha, M. Lebert, Y.-Y. He, R. Buffoni-Hall, N. V. J. de Bakker, J. van de Staaij and R. B. Meijkamp (2002) The role of UV-B radiation in aquatic and terrestrial ecosystems—an experimental and functional analysis of the evolution of UV-absorbing compounds. *J. Photochem. Photobiol. B: Biol.* **66**, 2–12.
31. Searles, P. S., S. D. Flint, S. B. Diaz, M. C. Rousseaux, C. L. Ballaré and M. M. Caldwell (2002) Plant response to solar ultraviolet-B radiation in a southern South American *Sphagnum* peatland. *J. Ecol.* **90**, 704–713.
32. Caldwell, M. M., C. L. Ballaré, J. F. Bornman, S. D. Flint, L. O. Björn, A. H. Teramura, G. Kulandaivelu and M. Tevini (2003) Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climatic change factors. *Photochem. Photobiol. Sci.* **2**, 29–38.
33. Flint, S. D., R. J. Ryel and M. M. Caldwell (2003) Ecosystem UV-B experiments in terrestrial communities: a review of recent findings and methodologies. *Agric. Forest Meteor.* **120**, 177–189.
34. Kakani, V. G., K. R. Reddy, D. Zhao and K. Sailaja (2003) Field crop responses to ultraviolet-B radiation, a review. *Agric. Forest Meteor.* **120**, 191–218.

35. Krupa, S. V. (2003) Joint effects of elevated levels of ultraviolet-B radiation, carbon dioxide and ozone on plants. *Photochem. Photobiol.* **78**, 535–542.
36. Bassman, J. H. (2004) Ecosystem consequences of enhanced solar ultraviolet radiation: secondary plant metabolites as mediators of multiple trophic interactions in terrestrial plant communities. *Photochem. Photobiol.* **79**, 382–398.
37. Giordano, C. V., A. Galatro, S. Puntarulo and C. L. Ballaré (2004) The inhibitory effects of UV-B radiation (280–315 nm) on *Gunnera magellanica* growth correlate with increased DNA damage but not with oxidative damage to lipids. *Plant Cell Environ.* **27**, 1415–1423.
38. Shulski, M. D., E. A. Walter-Shea, K. G. Hubbard, G. Y. Yuen and G. Horst (2004) Penetration of photosynthetically active and ultraviolet radiation into alfalfa and tall fescue canopies. *Agron. J.* **96**, 1562–1571.
39. Weinig, C., K. A. Gravuer, N. C. Kane and J. A. Schmitt (2004) Testing adaptive plasticity to UV: costs and benefits of stem elongation and light-induced phenolics. *Evolution* **58**, 2645–2656.
40. Krizek, D. T. (2004) Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation. *Photochem. Photobiol.* **79**, 307–315.
41. Furness, N. H., P. A. Jolliffe and M. K. Upadhyaya (2005) Ultraviolet-B radiation and plant competition: experimental approaches and underlying mechanisms. *Photochem. Photobiol.* **81**, 1026–1037.
42. Grant, R. H. (2005) High UVB exposures in the continental USA: towards realistic short term exposure regimes for plant effects research. *Photochem. Photobiol.* **81**, 1038–1046.
43. Flint, S. D. and M. M. Caldwell (2003) A biological spectral weighting function for ozone depletion research with higher plants. *Physiol. Plant.* **117**, 137–144.
44. Flint, S. D., P. S. Searles and M. M. Caldwell (2004) Field testing of biological spectral weighting functions for induction of UV-absorbing compounds in higher plants. *Photochem. Photobiol.* **79**, 399–403.
45. Krizek, D. T., H. D. Clark and R. M. Mirecki (2005) Spectral properties of selected UV-blocking and UV-transmitting covering materials with application for production of high-value crops in high tunnels. *Photochem. Photobiol.* **81**, 1047–1051.
46. Raviv, M. and Y. Antignus (2004) UV radiation effects on pathogens and insect pests of greenhouse-grown crops. *Photochem. Photobiol.* **79**, 219–226.
47. Antignus, Y. and D. Ben-Yakir (2004) Ultraviolet-absorbing barriers, an efficient integrated pest management tool to protect greenhouses from insects and virus diseases. In *Insect Pest Management* (Edited by A. R. Horowitz and I. Ishaaya), pp. 319–335. Springer-Verlag, Berlin, Heidelberg.
48. Antignus, Y., M. Lapidot and S. Cohen (2004) Interference with ultraviolet vision of insects to impede insect pests and insect-borne viruses. In *Virus-Insect Plant Interactions* (Edited by K. F. Harris, O. P. Smith and J. E. Duffus), pp. 331–350. Academic Press, San Diego.
49. Paul, N. D., R. J. Jacobson, A. Taylor, J. J. Wargent and J. P. Moore (2005) The use of wavelength selective plastic cladding materials in horticulture: understanding of crop and fungal responses through the assessment of biological spectral weighting functions. *Photochem. Photobiol.* **81**, 1052–1060.
50. Gerhardt, K. E., M. I. Wilson and B. M. Greenberg (2005) Ultraviolet wavelength dependence of photomorphological and photosynthetic responses in *Brassica napus* and *Arabidopsis thaliana*. *Photochem. Photobiol.* **81**, 1061–1068.
51. Shinkle, J. R. and P. W. Barnes (2005) Comparative photobiology of growth responses of two UV-B wavebands and UV-C in dim-red-light- and white-light-grown cucumber (*Cucumis sativus* L.) seedlings: physiological evidence for photoreactivation. *Photochem. Photobiol.* **81**, 1069–1074.
52. Middleton, E. M., M. S. Kim, D. T. Krizek and R. K. S. Bajwa (2005) Evaluating UV-B effects and EDU protection in soybean leaves using fluorescence. *Photochem. Photobiol.* **81**, 1075–1085.
53. Ruhland, C. T., F. S. Xiong, W. D. Clark and T. A. Day (2005) The influence of ultraviolet-B radiation on growth, hydroxycinnamic acids and flavonoids of *Deschampsia antarctica* during springtime ozone depletion in Antarctica. *Photochem. Photobiol.* **81**, 1086–1093.
54. L'Hirondelle, S. J. and W. D. Binder (2005) Temperature stress tolerance of conifer seedlings after exposure to UV-B radiation. *Photochem. Photobiol.* **81**, 1094–1100.
55. Teklemariam, T. and T. J. Blake (2003) Effects of UV-B preconditioning on heat tolerance of cucumber (*Cucumis sativus* L.) *Environ. Exp. Bot.* **50**, 169–182.
56. Chalker-Scott, L. and J. D. Scott (2004) Elevated ultraviolet-B radiation induces cross- protection to cold in leaves of rhododendron under field conditions. *Photochem. Photobiol.* **79**, 199–204.
57. Caasi-Lit, M. T. (2005) Effects of crude and partially purified extracts from UV-B–irradiated rice leaves on *Helicoverpa armigera* (Hübner). *Photochem. Photobiol.* **81**, 1101–1106.
58. Warren, J. M., J. H. Bassman, J. K. Fellman, D. S. Mattinson and S. Eigenbrode (2003) Ultraviolet-B radiation alters phenolic salicylate and flavonoid composition of *Populus trichocarpa* leaves. **23,** 527–535.